



## Human population growth offsets climate-driven increase in woody vegetation in sub-Saharan Africa

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*Published in:*  
Nature Ecology & Evolution

*DOI:*  
[10.1038/s41559-017-0081](https://doi.org/10.1038/s41559-017-0081)

*Publication date:*  
2017

*Document version*  
Peer reviewed version

*Citation for published version (APA):*  
Brandt, M. S., Rasmussen, K., Peñuelas, J., Tian, F., Schurgers, G., Verger, A., ... Fensholt, R. (2017). Human population growth offsets climate-driven increase in woody vegetation in sub-Saharan Africa. *Nature Ecology & Evolution*, 1, [0081 ]. <https://doi.org/10.1038/s41559-017-0081>

1 Revised Version 2

2 **Human population growth offsets climate-driven increase in woody vegetation in sub-Saharan Africa**

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22

## 23 **Abstract**

24 The rapidly growing human population in sub-Saharan Africa generates an increasing demand for agricultural  
25 land and forest products which presumably leads to deforestation. Conversely, a greening of African drylands  
26 has been reported but this has been difficult to associate with changes in woody vegetation. There is thus an in-  
27 complete understanding of how woody vegetation responds to socio-economic and environmental change. Here  
28 we used a passive microwave Earth Observation data set to document two different trends in woody cover for  
29 1992-2011: an increase of 36% on the land area (6,870,000 km<sup>2</sup>), largely in drylands, and a decrease of 11%  
30 (2,150,000 km<sup>2</sup>), mostly in humid zones. Increases in woody cover were associated with areas of low population  
31 growth and driven by increases in CO<sub>2</sub> in the humid zones and by increases in precipitation in drylands, whereas  
32 decreases in woody cover were associated with areas of high population growth. The spatially distinct pattern of  
33 these opposing trends reflects (1) the natural response of vegetation to precipitation and atmospheric CO<sub>2</sub> and (2)  
34 deforestation in humid areas, minor in size but important for ecosystem services, such as biodiversity and carbon  
35 stocks. This nuanced picture of changes in woody cover challenges widely held views of a general and ongoing  
36 reduction of the woody vegetation in Africa.

## 37 **Introduction**

38 Africa's human population has increased from about 230 million in 1950 to over 1000 million in 2010 and is ex-  
39 pected to grow to as high as 5700 million by the end of the 21<sup>st</sup> century<sup>1</sup>. This growth has led to the expansion of  
40 agricultural land and the reduction of natural forests and other woody vegetation<sup>2,3,6</sup>, affecting biodiversity and  
41 carbon storage<sup>3</sup>. Severe droughts in recent decades have also had an adverse impact on humid and sub-humid  
42 forested areas<sup>7</sup>. In contrast, studies of drylands have shown an increase in vegetation productivity over the last  
43 30 years<sup>4,8</sup>, also highlighting the importance of drylands for global carbon variability and as land CO<sub>2</sub> sink<sup>9</sup>.  
44 Whether this increase in vegetation productivity is driven by the growth of woody vegetation and/or by an in-  
45 crease in productivity of herbaceous vegetation is not clear. This is because the scattered nature of woody plants  
46 in drylands is very different from forests with closed canopies and challenging to detect with optical satellite im-  
47 agery at regional to continental scales<sup>10,11</sup>. Previous studies have used vegetation indices as proxies for net pri-  
48 mary productivity, but these indices measure the photosynthetically active part of the vegetation and most stud-  
49 ies do not distinguish between woody and herbaceous vegetation<sup>12,13</sup>. Furthermore, studies of deforestation in hu-  
50 mid areas traditionally report the presence or absence of forests<sup>3</sup> and do not assess gradual changes in forest bio-  
51 mass within existing forests (e.g., forest degradation). They are also based on temporal snapshots of satellite im-  
52 agery at a higher spatial resolution and only capture forests based on given definitions, e.g. tree height and cano-  
53 py cover percentage<sup>3,14</sup>, which substantially underestimate shrubs and scattered trees in drylands<sup>10</sup>. Conse-  
54 quently, little quantitative information is available about the state, rate, and drivers of change in the cover of  
55 woody vegetation at the scale of the African continent. This information is crucial for ensuring that the design of  
56 natural resource management in relation to deforestation and desertification is based on observations rather than  
57 those based on narratives.

58

## 59 **Results**

### 60 **Africa's woody cover is under change**

61 We used a new passive microwave Earth Observation (EO) data set (Vegetation Optical Depth, VOD) that cap-

62 tures continuous changes in the coverage of canopies of all woody phanerophytes, regardless of size, in both dry-  
 63 lands and humid areas<sup>15-17</sup>. We applied VOD as a proxy for annual woody cover and documented changes in  
 64 Africa's woody vegetation between 1992 and 2011, with a special focus on the changes in drylands and humid  
 65 areas (defined by the ratio between annual precipitation and potential evapotranspiration, Supplementary Fig.  
 66 1a). Woody vegetation changed significantly (slope of linear regression,  $p < 0.05$ ) during 1992–2011 in approxi-  
 67 mately half of sub-Saharan Africa (47% of land areas). A majority (77%) of the significant trends were positive,  
 68 covering 36% of sub-Saharan Africa and representing an overall increase of 2.1 woody cover (%) (Fig. 1a).  
 69 Most (70%) of the significant positive changes were in drylands covering approximately 4 900 000 km<sup>2</sup> (overall  
 70 change +2.9 woody cover (%)), mainly in the Sahel and southern Africa<sup>18-20</sup> (Fig. 2a). Positive trends are also  
 71 observed in the humid zones to a much smaller extent (2 100 000 km<sup>2</sup>), with an overall change of +0.8 woody  
 72 cover (%). Negative changes affected 11% of sub-Saharan Africa, of which 75% were in humid areas (approxi-  
 73 mately 1 600 000 km<sup>2</sup> in humid zones and 530 000 km<sup>2</sup> in drylands). The decline in woody cover primarily af-  
 74 fected areas that are also characterized by high carbon stocks (Supplementary Figs 2a, 2b), suggesting that areas  
 75 with the largest carbon sinks have been disturbed at the fastest rate. The classification of woody cover change in-  
 76 to bioclimate zones<sup>21</sup> confirms the overall tendency with larger increases in drier zones (except extremely hot xe-  
 77 ric) and lower increases and decreases in moister zones (Fig. 2d).

78

## 79 **Drivers of woody cover changes**

80 The positive changes in woody cover in Africa's drylands are significantly related to precipitation (Fig. 1a). In  
 81 contrast to herbaceous vegetation, woody plants can benefit from a higher variability and intensity of precipita-  
 82 tion<sup>22</sup>, as in southern Africa and the Sahel (Supplementary Fig. 1c). The dependence on precipitation was corro-  
 83 borated with simulations of the vegetation using the dynamic vegetation model LPJ-GUESS<sup>23</sup>, which simulated  
 84 an increase in woody biomass for 1992-2011, consistent with the satellite estimates of woody cover (Fig. 3). The  
 85 relative increase of both woody cover and biomass was largest in drylands, and factorial simulations of the indi-  
 86 vidual driving variables indicated that precipitation accounted for most of the simulated increase in woody bio-  
 87 mass in drylands such as the Sahel and southern Africa (Fig. 3, Supplementary Fig. 3). Increasing concentrations

88 of atmospheric CO<sub>2</sub> was a minor contributor to these dryland trends yet was the main variable driving the growth  
89 of woody vegetation in humid areas, enhancing primary production<sup>24</sup> (Fig. 3, Supplementary Figs. 2, 3). The ab-  
90 solute increase in woody biomass was largest in humid areas (mean increase of 0.04 kg C m<sup>-2</sup> y<sup>-1</sup> near the equa-  
91 tor, Supplementary Fig. 2), coinciding with overall large stocks of woody biomass. Solar radiation, nitrogen dep-  
92 osition and temperature had minor impacts on the changes in woody biomass (Supplementary Fig. 2).

93 This increase in woody vegetation driven by climate and CO<sub>2</sub>, however, was offset by anthropogenic impacts,  
94 especially in humid areas. The increase in woody cover in the VOD analysis was thus most pronounced in areas  
95 of low human population density and change (Fig. 4). Areas and countries with a higher population density and  
96 growth (Fig. 1b, Supplementary Fig. 1d) had decreases in VOD-based woody cover (Figs. 1a, 4, Supplementary  
97 Fig. 4), offsetting the climate-driven increases in other parts of the humid zones (Figs. 2c, 3). This separation in  
98 areas of high and low human pressure applied to both drylands and humid tropics. The average trend, however,  
99 remained positive in drylands, even in areas with strong population growth, but was negative in humid areas  
100 with strong population growth, regardless of the trends in precipitation and CO<sub>2</sub> (Fig. 2b, c). Populations in-  
101 creased by an average of 40 persons km<sup>-2</sup> over 20 years in areas where woody cover decreased supposedly due  
102 to agricultural expansion, logging, and other uses of woody products. In contrast, populations increased by an  
103 average of only 6 persons km<sup>-2</sup> in areas where woody cover increased. Human population increase was highest  
104 in moist and mesic bioclimate zones and woody cover changes were accordingly negative or low, whereas popu-  
105 lation growth was lower in xeric areas and woody cover increases were higher (Fig. 2d). At the continental scale,  
106 a simultaneous autoregressive model (SAR) explained nearly half of the spatial pattern of changes in woody cov-  
107 er in terms of changes in population and precipitation ( $r^2=0.46$ ), with population being more important than pre-  
108 cipitation (standardized slopes of -0.27 and 0.08, respectively) (Supplementary Table 1).

109

## 110 **Discussion**

111 The opposing trends in dry and humid zones have implications for our understanding of environmental change in  
112 sub-Saharan Africa. While areas of high population growth, mostly in humid zones, on average experience a de-

crease in woody vegetation, areas with low population growth on average experience an increase in woody vegetation, mainly driven by changes in precipitation and CO<sub>2</sub> concentrations. This latter increase is not captured in official forest statistics, since much of it takes place outside of humid forests.

This implies that the ‘problem’ of woody cover loss - and thus carbon stocks decreases - in the humid forest zones is at least partly balanced by an increase in drylands. ‘Bush encroachment’ in savannas of southern Africa, however, has traditionally been considered an undesired effect<sup>14,25</sup>. Since the VOD data used to estimate woody cover does not allow direct estimation of carbon stocks, the exact balance between gains and losses in carbon cannot be directly assessed in this study. Further work combining field measurements, ecosystem modelling and new satellite-based passive microwave sensors is required to further understand these linkages. In humid areas, woody biomass may actually increase without any change in woody cover.

The close relationship between population growth and decreased woody cover suggests that agricultural expansion, urbanization and wood fuel harvest were the main causes of the decrease in woody cover, as also found in studies of tropical deforestation<sup>3,26</sup>. The reduction in woody cover tends to primarily affect areas with high carbon stocks and other studies suggest that these are also areas characterized by the highest biological diversity<sup>27</sup>. There is, however, no simple relation between losses and gains in woody cover and biodiversity. While diversity and productivity of natural vegetation are generally positively correlated<sup>28</sup>, this does not exclude the possibility that great losses may be experienced in areas of deforestation, while only smaller gains are seen in drylands with increasing woody cover.

Due to the impact on land surface albedo, woody cover changes in dryland areas may trigger climate feed-backs. Since the hypothesized existence of a ‘biogeophysical feed-back’<sup>29</sup>, many studies have attempted to model such effects<sup>30,31</sup>, with some research claiming that man-made afforestation efforts would give rise to increased precipitation<sup>32</sup>. The extent of the observed increase in woody cover in African drylands may impact climate if the increase continues in the coming decades, and this altered feed-back should preferably be implemented and tested in regional climate models.

137

## 138 **Methods**

**VOD data and calibration to woody cover.** We define woody cover as the percentage of a given area covered by woody vegetation, including both leaf and woody components (stem/branches) of woody plant canopies. The unit is woody cover (%). The VOD data was retrieved from satellite passive microwave observations quantified as brightness temperature based on the NASA-VU Land Parameter Retrieval Model (LPRM)<sup>33</sup>. Three passive microwave sensors, i.e. the Special Sensor Microwave Imager, the Advanced Microwave Scanning Radiometer – Earth Observing System, and the radiometer of WindSat are used to form the long-term data set by applying a trend-preserving cumulative distribution function matching without changing the inter-annual variations and long-term trends of the original retrievals<sup>34,35</sup>. The merged long-term VOD data set was gridded at a 0.25° spatial resolution and monthly interval from 1992 to 2011 and is consistent between different sensors<sup>11</sup>. VOD is sensitive to the total aboveground water content in both the photosynthetic (foliar) and non-photosynthetic (woody) components of the vegetation stratum<sup>15,36</sup>. Soil moisture conditions are retrieved simultaneously with the VOD information in LPRM and large variations in soil moisture can influence the accuracy of VOD, especially for dense rainforest regions. Thus VOD values exceeding 1.2 are suggested to be excluded in vegetation studies<sup>16</sup>. The VOD signal has been separated from soil moisture and is used as a proxy for vegetation biomass globally<sup>34</sup>. The VOD seasonal variation is a combined effect of the seasonal dynamics of both herbaceous (including crops) and woody vegetation<sup>15</sup>. We used the annual minimum VOD values as a proxy for woody vegetation cover to minimize the influence of annual herbaceous vegetation<sup>10</sup> and avoided values exceeding 1.2 (Supplementary Fig. 5). Areas with perennial herbaceous vegetation may lead to an over-estimation of woody cover; however, the woody cover % is usually higher in these areas concealing the influence from the herbaceous plant understory. Also, VOD data have been used to estimate forest change in South America by limiting the range of VOD values to 0.6-1.2<sup>16</sup>. We did not restrict the VOD range to also include young trees and shrubs, which form an important part of the community of woody vegetation. Minimum VOD agrees well with field data based on a map of woody cover for Sahel ( $r^2=0.80$ )<sup>10</sup> (Supplementary Fig. 5). A global map calibrated with optical high spatial resolution images and also assessing smaller trees produced similar results<sup>37</sup> and was thus used to transform the annual minimum VOD to the unit woody cover (%) for further analyses ( $r^2=0.85$ , slope=0.86) (Supplementary Fig. 5). A third-degree polynomial regression was used for the transformation. Woody cover <10% was predicted with an exponential regression to avoid underestimation of very low values. The VOD is insensitive to the ef-



fects of atmospheric and cloud contamination, ensuring reliable retrievals in cloudy regions e.g. central Africa.

**Correlation between the trends in woody cover and changes in human population and precipitation.** Precipitation data were derived from the Climate Research Unit (CRU) (data set version 3.23), which is globally available for a 0.5° grid at monthly scale and is based on the upscaling of data from rain gauges<sup>38</sup>. CRU precipitation data intrinsically includes some uncertainty, as the number of stations used for each grid cell varies considerably between cells and years. Even though consistency with other data sets has been shown (DINKU) and it is the most widely used precipitation data set in dynamic vegetation modelling<sup>39</sup>, results have to be considered with caution<sup>7</sup>. We have tested the blended GPCP data set, without significant changes of the results, still it has to be noted that a linear trend analysis on annually summed data includes uncertainties and simplifications. We summed the monthly observations to obtain annual sums from 1992 to 2011 and resampled the data to 0.25° using a bicubic interpolation. Population data were acquired from Gridded Population of the World (GPW) v3<sup>40</sup>, which includes estimates for 1990, 1995, 2000, 2005, and 2010, gridded with an output resolution of 2.5 arc-minutes, resampled for this study to 0.25° (nearest neighbor). GPW population data were acquired from national statistical offices and gridded based on the proportional method, which allocates population counts to grid cells based on the proportion of each administrative areal unit that overlaps the cell. The gridded counts for existing census years are then projected to the set of output years based on a simple model of population growth. The modeling was thus not based on any additional layers of data, such as land cover, avoiding potential problems of endogeneity between VOD and simulated population grids. A linear trend analysis was conducted for annual woody cover and precipitation data, and the slope multiplied with the number of years to retrieve the absolute change over time in the corresponding unit, facilitating the direct comparison with the human population data. We quantified the relationships between the changes in woody cover (estimated by VOD), population increase (GPW), and precipitation (CRU) by applying a simultaneous autoregressive model (SAR) (spatial error type<sup>41</sup>) to the three gridded data sets. The SAR model accounts for spatial autocorrelation and uses change in woody cover as response and log(change in population) and change in precipitation as explanatory variables. The logarithm of the human population data was applied since the relation between woody cover changes and human population is non-linear at pixel scale, i.e. if a high number of population is reached (mostly in cities), the woody

cover stops to decrease further. Standardized variables were used to enable model coefficients inter-comparison  
(standardized variable = (variable - mean) / standard deviation).

Fires frequently occur in most African ecosystems. However, at the spatial and temporal scale of our analysis, we do not expect changes in fire regimes as a major cause of changes in woody cover in itself but rather as a consequence of human induced deforestation and land use change<sup>42</sup>.

**Dynamic ecosystem model.** The dynamic ecosystem model LPJ-GUESS<sup>23</sup> was applied to simulate changes in woody-biomass carbon in natural vegetation for 1992-2011. LPJ-GUESS simulates the distribution of plant functional types, and each type is represented by four pools of biomass carbon: leaves, roots, sapwood, and heartwood. The latter two were added to represent the amounts of stem (wood) carbon. This variable is closely related to the woody cover estimated by VOD, but especially in tropical forests, differences are expected, as VOD is not able to fully penetrate the tree crowns<sup>43</sup>. Simulations were run for 1992-2011, applying monthly climate data (temperature, precipitation, sunshine duration) from meteorological stations, gridded to 0.5°×0.5° resolution (CRU TS 3.21<sup>37</sup>), monthly model-derived estimates for nitrogen deposition<sup>44</sup>, and annual mean atmospheric CO<sub>2</sub> concentrations<sup>45,46</sup> based on ice-core data and atmospheric observations as forcing. Land use and land use change were not accounted for in the simulations, which were only applied to quantify the changes in natural vegetation. The simulations were preceded by a two-stage spinup: For the first stage, vegetation growth starts from bare-ground conditions, using climatic data for 1901-1930, and CO<sub>2</sub> levels were kept constant at the concentration for 1901. For the second stage, representing 1901-1991, the actual climate data, atmospheric CO<sub>2</sub> concentration and N deposition were used.

In addition to a full simulation with the forcing as described above, five factorial simulations were performed to separate the impact of individual driving variables. Only one of the four parameters (temperature, precipitation, radiation, or CO<sub>2</sub>) was applied using the transient data as described above, whereas the other three parameters used a climatology for 1992-2011, applying monthly means over this 20-year period for the climatic parameters and an annual mean for CO<sub>2</sub>. In the fifth factorial simulation, similar to the transient CO<sub>2</sub> simulation above, the changing CO<sub>2</sub> concentration was combined with a climatology for N deposition, to separate the impacts of atmospheric CO<sub>2</sub> and N deposition on the CO<sub>2</sub> fertilization. These simulations were applied to determine the im-

218 pact of the individual driving variables on the simulated trend.

219 **Data availability** CRU precipitation data are available from the University of East Anglia  
220 (<http://www.cru.uea.ac.uk/>). The global tree cover map is available from the Geospatial Information Authority of  
221 Japan, Chiba University (<http://www.iscgm.org/gm/ptc.html#use>). VOD raster data are provided and available  
222 by Yi Liu, University of New South Wales. Gridded population maps are provided by CIESIN (<http://sedac.ciesin.columbia.edu/>). Humidity zones are available from <http://www.grid.unep.ch/index.php>.

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## 225 **References**

1. Gerland, P. et al. World population stabilization unlikely this century. *Science* 346, 234–237 (2014).
2. Lambin, E. F. & Meyfroidt, P. Global land use change, economic globalization, and the looming land scarcity. *Proc. Natl. Acad. Sci.* 108, 3465–3472 (2011).
3. Hansen, M. C. et al. High-Resolution Global Maps of 21st-Century Forest Cover Change. *Science* 342, 850–853 (2013).
6. Mayaux, P. et al. State and evolution of the African rainforests between 1990 and 2010. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 368, 20120300 (2013).
4. Fensholt, R. et al. Greenness in semi-arid areas across the globe 1981–2007 — an Earth Observing Satellite based analysis of trends and drivers. *Remote Sens. Environ.* 121, 144–158 (2012).
5. Andela, N., Liu, Y. Y., van Dijk, A. I. J. M., de Jeu, R. A. M. & McVicar, T. R. Global changes in dryland vegetation dynamics (1988–2008) assessed by satellite remote sensing: comparing a new passive microwave vegetation density record with reflective greenness data. *Biogeosciences* 10, 6657–6676 (2013).
7. Zhou, L. et al. Widespread decline of Congo rainforest greenness in the past decade. *Nature* 509, 86–90

(2014).

8. Kaptué, A. T., Prihodko, L. & Hanan, N. P. On regreening and degradation in Sahelian watersheds. *Proc. Natl. Acad. Sci.* 201509645 (2015). doi:10.1073/pnas.1509645112
9. Ahlström, A. et al. The dominant role of semi-arid ecosystems in the trend and variability of the land CO<sub>2</sub> sink. *Science* 348, 895–899 (2015).
10. Brandt, M. et al. Woody plant cover estimation in drylands from Earth Observation based seasonal metrics. *Remote Sens. Environ.* 172, 28–38 (2016).
11. Donohue, R. J., McVicar, T. R. & Roderick, M. L. Climate-related trends in Australian vegetation cover as inferred from satellite observations, 1981–2006. *Global Change Biology* 15, 1025–1039 (2009).
12. Zhu, Z. et al. Greening of the Earth and its drivers. *Nature Clim. Change* advance online publication, (2016).
13. Kolby Smith, W. et al. Large divergence of satellite and Earth system model estimates of global terrestrial CO<sub>2</sub> fertilization. *Nature Climate Change* 6, 306–310 (2015).
14. Shimada, M. et al. New global forest/non-forest maps from ALOS PALSAR data (2007–2010). *Remote Sens. Environ.* 155, 13–31 (2014).
15. Tian, F., Brandt, M., Liu, Y. Y., Rasmussen, K. & Fensholt, R. Mapping gains and losses in woody vegetation across global tropical drylands. *Global Change Biology* (2016). doi:10.1111/gcb.13464.
16. van Marle, M. J. E., van der Werf, G. R., de Jeu, R. A. M. & Liu, Y. Y. Annual South American forest loss estimates based on passive microwave remote sensing (1990–2010). *Biogeosciences* 13, 609–624 (2016).
17. Jones, M. O., Kimball, J. S. & Jones, L. A. Satellite microwave detection of boreal forest recovery from the extreme 2004 wildfires in Alaska and Canada. *Glob. Change Biol.* 19, 3111–3122 (2013).
18. Brandt, M. et al. Ground- and satellite-based evidence of the biophysical mechanisms behind the greening Sahel. *Glob. Change Biol.* 21, 1610–1620 (2015).

19. Wigley, B. J., Bond, W. J. & Hoffman, M. T. Thicket expansion in a South African savanna under divergent land use: local vs. global drivers? *Glob. Change Biol.* 16, 964–976 (2010).
20. Mitchard, E. T. A. & Flintrop, C. M. Woody encroachment and forest degradation in sub-Saharan Africa's woodlands and savannas 1982–2006. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 368, 20120406 (2013).
21. Metzger, M. J. et al. A high-resolution bioclimate map of the world: a unifying framework for global biodiversity research and monitoring. *Global Ecology and Biogeography* 22, 630–638 (2013).
22. Gherardi, L. A. & Sala, O. E. Enhanced precipitation variability decreases grass- and increases shrub-productivity. *Proc. Natl. Acad. Sci.* 112, 12735–12740 (2015).
23. Smith, B. et al. Implications of incorporating N cycling and N limitations on primary production in an individual-based dynamic vegetation model. *Biogeosciences* 11, 2027–2054 (2014).
24. Yang, Y., Donohue, R. J., McVicar, T. R., Roderick, M. L. & Beck, H. E. Long-term CO<sub>2</sub> fertilization increases vegetation productivity and has little effect on hydrological partitioning in tropical rainforests. *J. Geophys. Res. Biogeosci.* 2016JG003475 (2016). doi:10.1002/2016JG003475
25. Bond, W. J. & Midgley, G. F. Carbon dioxide and the uneasy interactions of trees and savannah grasses. *Phil. Trans. R. Soc. B* 367, 601–612 (2012).
26. Lambin, E. F. & Geist, H. J. *Land-Use and Land-Cover Change: Local Processes and Global Impacts.* (Springer Science & Business Media, 2008).
27. Cincotta, R. P., Wisniewski, J. & Engelman, R. Human population in the biodiversity hotspots. *Nature* 404, 990–992 (2000).
28. Willig, M. R. Biodiversity and Productivity. *Science* 333, 1709–1710 (2011).
29. Charney, J. G., Stone, P. H. & Quirk, W. J. Drought in the Sahara: a biogeophysical feedback mechanism. *Science* 187, 434–435 (1975).

30. Taylor, C. M., Lambin, E. F., Stephenne, N., Harding, R. J. & Essery, R. L. H. The Influence of Land Use Change on Climate in the Sahel. *Journal of Climate* 15, 3615–3629 (2002).
31. Wu, M. et al. Vegetation–climate feedbacks modulate rainfall patterns in Africa under future climate change. *Earth System Dynamics* 7, 627–647 (2016).
32. Abiodun, B. J., Adeyewa, Z. D., Oguntunde, P. G., Salami, A. T. & Ajayi, V. O. Modeling the impacts of re-forestation on future climate in West Africa. *Theoretical and Applied Climatology* 110, 77–96 (2012).
33. Owe, M., de Jeu, R. & Holmes, T. Multisensor historical climatology of satellite-derived global land surface moisture. *J. Geophys. Res.* 113, F01002 (2008).
34. Liu, Y. Y. et al. Recent reversal in loss of global terrestrial biomass. *Nat. Clim. Change* 5, 470–474 (2015).
35. Liu, Y. Y. et al. Trend-preserving blending of passive and active microwave soil moisture retrievals. *Remote Sens. Environ.* 123, 280–297 (2012).
36. Guglielmetti, M. et al. Measured microwave radiative transfer properties of a deciduous forest canopy. *Remote Sens. Environ.* 109, 523–532 (2007).
37. Kobayashi, T., Tsens-Ayush, J. & Tateishi, R. A New Tree Cover Percentage Map in Eurasia at 500 m Resolution Using MODIS Data. *Remote Sens.* 6, 209–232 (2013).
38. Harris, I., Jones, P. d., Osborn, T. j. & Lister, D. h. Updated high-resolution grids of monthly climatic observations – the CRU TS3.10 Dataset. *Int. J. Climatol.* 34, 623–642 (2014).
- 1.Dinku, T., Connor, S. J., Ceccato, P. & Ropelewski, C. F. Comparison of global gridded precipitation products over a mountainous region of Africa. *Int. J. Climatol.* 28, 1627–1638 (2008).
39. Poulter, B. et al. Contribution of semi-arid ecosystems to interannual variability of the global carbon cycle. *Nature* 509, 600–603 (2014).
40. Doxsey-Whitfield, E. et al. Taking Advantage of the Improved Availability of Census Data: A First Look at

the Gridded Population of the World, Version 4. *Pap. Appl. Geogr.* 1, 226–234 (2015).

41. Kissling, W. D. & Carl, G. Spatial autocorrelation and the selection of simultaneous autoregressive models. *Glob. Ecol. Biogeogr.* 17, 59–71 (2008).
42. Andela, N. & van der Werf, G. R. Recent trends in African fires driven by cropland expansion and El Nino to La Nina transition. *Nature Clim. Change* 4, 791–795 (2014).
43. Jones, M. O., Kimball, J. S. & Nemani, R. R. Asynchronous Amazon forest canopy phenology indicates adaptation to both water and light availability. *Environ. Res. Lett.* 9, 124021 (2014).
44. Lamarque, J.-F. et al. Multi-model mean nitrogen and sulfur deposition from the Atmospheric Chemistry and Climate Model Intercomparison Project (ACCMIP): evaluation of historical and projected future changes. *Atmospheric Chemistry and Physics* 13, 7997–8018 (2013).
45. Etheridge, D. M. et al. Natural and anthropogenic changes in atmospheric CO<sub>2</sub> over the last 1000 years from air in Antarctic ice and firn. *Journal of Geophysical Research: Atmospheres* 101, 4115–4128 (1996).
46. Keeling, C. D., Whorf, T. P., Wahlen, M. & van der Plichtt, J. Interannual extremes in the rate of rise of atmospheric carbon dioxide since 1980. *Nature* 375, 666–670 (1995).

226 **Acknowledgements** M.B. received funding from the European Union's Horizon 2020 Research and Innovation  
227 program under Marie Skłodowska-Curie grant agreement No. [656564]. We thank Yi Y. Liu for providing the  
228 VOD data. A.V. and J.P. acknowledge support from the European Research Council Synergy grant ERC-2013-  
229 SYG-610028, IMBALANCE-P. The global tree cover map was obtained from  
230 <http://www.iscgm.org/gm/ptc.html#use> and the copyright is at the Geospatial Information Authority of Japan,  
231 Chiba University and collaborating organizations.

232

233 **Author Contributions** M.B., R.F., F.T. and A.V. designed the study. M.B. (VOD) and G.S. (ecosystem model)  
234 conducted the analyses with support by F.T., J.P., R.F. and J.P.. K.R. and M.B. drafted the manuscript with con-  
235 tributions by all authors.

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239 clare no competing financial interests.



240 **Figure legends:**

241 **Figure 1 | Changes in woody vegetation and human population over two decades.** **a**, Significant trends of  
242 woody cover (VOD) for 1992-2011, separated by the presence or absence of a significant ( $p < 0.05$ ) pearson cor-  
243 relation with cumulative 2-year precipitation during this period. **b**, Changes in human populations for 1990-  
244 2010. The maps in a and b share a clear pattern, especially areas with a decrease in woody cover, and no relation  
245 to precipitation coincide with a high population pressure. **c**, SAR model of the changes between woody cover,  
246 precipitation (both 1992-2011), and population (1990-2010). The units are expressed as change in the corre-  
247 sponding unit over the period of analysis.

248

249 **Figure 2 | Changes in woody cover (VOD) in different humidity zones.** **a**, Areas with changes in woody cov-  
250 er (linear regression of change in woody cover for 1992-2011). Annual profiles of woody cover for areas of stat-  
251 istically significant changes in woody cover in **b**, drylands and **c**, the humid areas of sub-Saharan Africa (Supple-  
252 mentary Fig. 1a). Black lines characterize areas of high human population increase ( $>30$  persons km) and grey  
253 lines areas of low human population increase ( $<10$  persons km). **d**, Woody cover and human population changes  
254 are grouped according to bioclimatic zones<sup>21</sup>.

255

256 **Figure 3 | Climatic drivers of changes in woody cover and biomass in sub-Saharan Africa.** Relative trends  
257 (% of mean year-1) for 1992-2011 in woody cover (estimated with VOD) and woody biomass (simulated with  
258 LPJ-GUESS) had similar patterns of change from north to south. The trends of woody biomass were mainly  
259 driven by CO<sub>2</sub> (humid areas) and precipitation (drylands) (Supplementary Figs. 2, 3).

260

261 **Figure 4 | Links between changes in woody cover and human population.** Intervals of mean population den-  
262 sity (1990-2010, Supplementary Fig. 1d) were used to group the changes in woody cover (VOD) associated with  
263 population increases and the number of pixels showing significant woody cover change. A Chi-squared test be-

264 tween woody cover and population change indicated the statistically significant dependency between the two  
265 variables.

266 **Supplementary Figure 1 | Humidity zones, changes in woody cover, trends in precipitation variability, and**  
267 **mean population density. a,** Humidity zones showing Africa's drylands (arid, semi-arid, and dry-subhumid re-  
268 gions) and humid areas. These zones are based on the ratio between annual precipitation and potential evapo-  
269 transpiration for 1951-1980 and were obtained from <http://www.grid.unep.ch/index.php>. **b,** Absolute changes in  
270 woody cover (%) (estimated from annual VOD minimum) for 1992-2011. **c,** Significant ( $p<0.05$ ) slope of linear  
271 regression of the annual coefficient of variation (CV) of CRU precipitation for 1992-2011 showing an increasing  
272 CV in southern Africa and parts of the Sahel. **d,** Mean population density for 1990-2010.

273  
274 **Supplementary Figure 2 | Trends of woody biomass and their drivers. a,** Mean woody cover (VOD) and **b,**  
275 Mean woody-biomass carbon (LPJ-GUESS) averaged per latitude. Differences are due to the different variables  
276 (woody cover vs total woody aboveground biomass, which differs mostly in humid forests because most woody  
277 material is stored in the stems hidden below the canopy), the saturation of VOD in the humid forests, and the  
278 poor capability of LPJ-GUESS to assess dryland shrubs, which omits large parts of southern Africa's woody veg-  
279 etation. **b,** The deviation from the inter-annual mean woody biomass shows a steady temporal increase in woody  
280 biomass. **c,** The total trends of woody biomass from north to south confirm the positive trend. The relative ef-  
281 fects of CO<sub>2</sub>, precipitation, radiation, and temperature on the trends identify CO<sub>2</sub> and precipitation as the main  
282 drivers.

283  
284 **Supplementary Figure 3 | Drivers of simulated trends of woody biomass (LPJ-GUESS). a, b,** Deviation  
285 from the mean for 1992-2011. **c, d,** Contribution of CO<sub>2</sub> and precipitation to the total trend. A negative value in-  
286 dicates an opposing trend and a positive value implies a high contribution to the total trend. CO<sub>2</sub> is identified as  
287 the dominant driver of the trends of woody biomass in humid areas, and precipitation is the dominant driver in  
288 drylands. Gray indicates non-significant trends.

289

290 **Supplementary Figure 4 | Changes in woody cover and human population by country.** Note that not only  
291 forests but all woody vegetation is captured, so these statistics are not comparable with forest losses and gains.  
292 Moreover, a change does not imply a replacement of a forest by a non-forested area.

293

294 **Supplementary Figure 5 | VOD and woody cover calibration and validation. a,** Raw annual VOD minimum  
295 is plotted against the woody cover map (<http://www.iscgm.org/gm/ptc.html#use>) which was used for transform-  
296 ing VOD minimum to the unit woody cover for sub-Saharan Africa. A third-degree polynomial regression was  
297 used for the transformation. Woody cover <10% was predicted with an exponential regression to avoid underes-  
298 timating very low values. **b,** The predicted woody cover map (using VOD) agrees well with the global map<sup>37</sup>  
299 ( $r^2=0.85$ , slope=0.86) and the unit woody cover (%) was thus used throughout the manuscript. **c,** For validation  
300 purpose, VOD minimum is plotted against a field data trained woody cover map of Sahel<sup>10</sup>. **d,** The mean woody  
301 cover estimated with VOD minimum is shown.

302

303 **Supplementary Table 1 | SAR model of the changes in woody cover.** Response variable: VOD (woody-cover  
304 change, 1992-2011). Explanatory variables: log(change in population) (persons km<sup>-2</sup>, 1990-2010), log(popula-  
305 tion density) (persons km<sup>-2</sup>, 1990-2010), change in precipitation (mm year<sup>-1</sup>, 1992-2011), and mean annual pre-  
306 cipitation (mm year<sup>-1</sup>, 1992-2011).

307

308 **Supplementary Figure 6 | Flowchart of the applied data sets and methods.**